Published in: Soil Biology & Biochemistry (2009), vol. 41, pp. 2038-2043.
Status: Postprint (Author's version)

Niche differentiation among neotropical soldierless soil-feeding termites revealed by stable isotope ratios

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Abstract

Termites represent one of the most abundant belowground animal taxa in tropical rainforests, where their species richness is much higher than in any other ecosystem. This high diversity in soil ecosystems is however difficult to explain by classical Hutchinsonian niche theory, as there is little evidence for spatial or temporal separation between species. Using $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios, we tested if resource partitioning along the humifkation gradient occurs in neotropical soldierless termites of the *Anoplotermes*-group. Two distinct sites were investigated to check if interspecific differences are transposable between sites. Significant differences in $\delta^{15}N$ were found between species of the *Anoplotermes*-group. Although some species displayed higher intersite $\delta^{15}N$ variation than others, species-average $\delta^{15}N$ values for both sites were highly correlated, showing that sympatric soldierless soil-feeding termites feed on distinct components of the soil. Our data also suggest that some species are more likely to shift along this gradient than others, in response to overall habitat conditions or to the presence of competitors. Feeding niche differentiation can therefore account for the high species richness and diversity of soldierless soil-feeding termites in neotropical rainforests.

Keywords : *Anoplotermes* ; Termitidae ; isoptera ; resource partitioning ; food web ; decomposition gradient

1. Introduction

Termites are major decomposers of organic matter in tropical ecosystems (Holt and Lepage, 2000), where they constitute a large part of the animal biomass (Fittkau and Klinge, 1973; Martius, 1994; Eggleton et al., 1996). Termite species have been distributed among "feeding groups" or "functional taxonomic groups", mainly based on the microhabitat in which foragers are found and observations of feeding habits and gut content (Eggleton et al., 1996; Bignell and Eggleton, 2000; Donovan et al., 2001 ; Gathorne-Hardy et al., 2002; Davies et al., 2003a). For instance, Donovan et al. (2001) recognized four feeding groups corresponding to an increasing humification of the feeding substrate. Wood feeders constitute groups I (non-Termitidae) and II (Termitidae), whereas soil-feeding Termitidae constitute groups III and IV. Anatomical features (sclerotized enteric valve and absence of mandible ridges) distinguish group IV from group III. Presumably, group III species feed at the soil-wood interface, whereas group IV species feed on more heavily mineralised soil (Donovan et al., 2001).

Soil-feeding taxa constitute a major part of termite species richness in tropical rainforests, especially in Africa and South America (review in Davies et al., 2003a). In the Neotropics, the *Anoplotermes*-group (subfamily Apicotermitinae), characterized by the absence of soldiers, is especially abundant and diversified. This group comprised, respectively, 34%, 45% and 30% of all termite species (33%, 35% and 34% of all encounters) recorded by ground transect sampling in a French Guiana, a Panamanian and a Central Amazonian rainforest (Davies et al., 2003b; Roisin et al., 2006; Ackerman et al., 2009). However, in spite of their richness and abundance, their biology remains poorly known. All are presumably interface- or soil-feeders (feeding group III or IV), but their precise food requirements remain largely unknown. Laboratory studies are hindered by the extreme difficulty in maintaining these termites under artificial conditions.

Usually, stable carbon isotope ratios ($^{13}C/^{12}C$) of animals are similar or slightly enriched compared to their diets, whereas stable nitrogen isotope ratios ($^{15}N/^{14}N$) (hereafter expressed as $\delta^{13}C$ and $\delta^{15}N$, see Methods) increase by 1.5-3‰ for each trophic level (McCutchan et al., 2003; Vanderklift and Ponsard, 2003; Hood-Nowotny and Knols, 2007). The picture is more complex in forest soils, where humification gradients are characterized by a gradual enrichment in ^{15}N resulting from a series of interrelated mechanisms, still incompletely understood, involving microorganisms and plant roots (Högberg, 1997; Kramer et al., 2003; Dijkstra et al., 2008). Therefore, the older and deeper the organic matter, the higher its $\delta^{15}N$ value (Piccolo et al., 1996; Martinelli et al., 1999; Krull et al., 2002; Billings and Richter, 2006; Hyodo et al., 2006, 2008). $\delta^{13}C$ values also increase down the soil profile but to a lesser extent and in a less consistent way (Tiunov, 2007). The low degree of enrichment in ^{13}C across trophic levels and down the soil profile makes the $\delta^{13}C$ ratio less useful than the $\delta^{15}N$ to infer the trophic structure of soil communities (Ponsard and Arditi, 2000), but the $\delta^{13}C$ may still help in distinguishing between trophic chains based on C3 versus C4 plants (Smith and Epstein, 1971 ; Boutton et al., 1983).

Stable isotope studies of termites revealed that $\delta^{15}N$ increases along the sequence wood → soil-wood interface → soil feeders (Tayasu et al., 1997, 1998, 2002a). In the Mbalmayo forest, Cameroon, $\delta^{15}N$ values are below 8 for wood feeders, but above 12 for mineral soil feeders (Tayasu et al., 1997). The same tendency is present in termites of the Darwin area, Australia, but with globally lower $\delta^{15}N$ values: wood feeders below 3, soil feeders above 5.5, interface feeders in between (Tayasu et al., 1998). In both sites, the $\delta^{15}N$ of wood-feeding termites is almost equal to the average $\delta^{15}N$ of their food source. Stable carbon isotopes show lesser discriminatory value than nitrogen, but $\delta^{13}C$ may separate grass- from wood-feeders (Tayasu et al., 1998, 2002b). These results are consistent with the classification into feeding groups proposed by Donovan et al. (2001), although there is ample overlap in $\delta^{15}N$ values between group I (non-Termitidae, all wood-feeding) and group II (wood-feeding Termitidae), and between group III and group IV (alleged interface- and soil-feeding Termitidae) (Eggleton and Tayasu, 2001). Although these studies encompassed a broad array of genera, they provided very few data on intra-generic variation and possible species-specific patterns. Nevertheless, they demonstrated the suitability of stable isotope analysis to situate termite niches in a gradient of humification.

The high diversity of decomposer animals in belowground ecosystems is difficult to explain by classical Hutchinsonian niche theory, as there is little evidence for spatial or temporal separation between species. A recently proposed mechanism to explain the diversity of detritivores is resource partitioning along the decomposition gradients of their food sources, revealed by $\delta^{15}N$ ratios (oribatid mites: Schneider et al., 2004; springtails: Chahartaghi et al., 2005; Hishi et al., 2007). Likewise, we hypothesized here that the high species richness of the *Anoplotermes*-group in neotropical rainforests could be explained by a differentiation of their feeding niches, which should be revealed by species-specific $\delta^{15}N$ values. A special feature of termites is that isotope effects (the difference in $\delta^{15}N$ between consumers and their diet) seem very variable, ranging from -1.6 to +8.8‰ (Tayasu et al., 1997). These authors suggested that fixation of atmospheric N_2 pulls this effect down for wood-feeding species, while selection of specific food particles from the soil pushes it up for soil feeders. As a consequence, the range of $\delta^{15}N$ values within a termite assemblage may greatly exceed that of their macroscopically identifiable food sources.

Considering that different sites are likely to display different overall isotopic signatures (Piccolo et al., 1996; Martinelli et al., 1999 ; Powers and Schlesinger, 2002), we carried out our investigations in two distinct forests. Even though the isotopic baseline might be different and influence the isotopic composition of soil-feeding termites, we expected that interspecific differences should be transposable between sites if trophic niche differentiation is an important structuring factor for the termite assemblage.

2. Materials and methods

2.3. Study site

Field work took place in two French Guiana forests: (i) the forest surrounding the Petit Saut dam (N 05°04', W 52°59') between 18 January and 21 February 2008; (ii) the Nouragues Nature Reserve (N 04°05', W 52°41') between 13 and 23 April 2008. Both forests experience about 3000 mm of rainfall per year, mostly distributed between January and June and with a drier season from September to November. The mean annual temperature is 26 °C. Both stations are covered by mature lowland forest on lateritic, well drained soil, with average canopy height reaching 30-40 m, whereas palm forests are patchily distributed in seasonally flooded areas. Petit Saut was mostly free of severe disturbance until 1994, when the area was partially inundated after the construction of the dam (for further details, see Cosson et al., 1999). The Nouragues is uninhabited and almost completely preserved from anthropogenic disturbances (for details see Bongers et al., 2001).

2.2. Sampling

Termites of the *Anoplotermes*-group were generally encountered either in the soil or in rotten wood. Two subsamples were taken from each foraging party: one series of individuals was prepared for isotopic analysis, as described below, whereas a voucher sample was kept in 80% alcohol for species identification. To reduce the risk of replicating samples from the same colony, we always kept a distance of at least 10 m between samples. Species were assigned to feeding groups according to the key of Donovan et al. (2001): as none of the *Anoplotermes*-group species possesses vestigial ridges on the right mandible molar plate, group IV was distinguished from group III by the sclerotisation of the enteric valve. The widespread rhinotermitid *Heterotermes tenuis* was sampled from both sites to provide reference data from a wood-feeding species (feeding group I).

2.3. Isotopic analysis

Between 10 and 50 termite workers were collected according to species size and pooled to obtain a sufficient amount of material for isotopic analysis. Only workers were taken into account to eliminate the effect of intercaste differences in isotopic values, which could bias cross-species comparisons. To avoid contamination by ingested material, all specimens were dissected and their digestive tract was removed. They were then dried at 60 °C for 24 h and airfreighted to Belgium. Dried samples were weighed in tin capsules and stored in a desiccator until analysed. Nitrogen and carbon stable isotope ratios were measured on a V.G. Optima (VG Instrument, UK) IR-MS coupled to an N-C-S elemental analyser (Carlo Erba, Italy). Stable isotope ratios were expressed as delta (δ) in ‰ according to

$$\delta X = \left(\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right) \times 1000$$

where R_{sample} is the isotopic ratio measured on the sample ($^{13}C/^{12}C$ or $^{15}N/^{14}N$), R_{standard} is the isotopic ratio of the international standard and X is the less abundant isotope of the considered element (^{13}C or ^{15}N). International standards were vPDB (Vienna Peedee Belemnite) and atmospheric N_2 for carbon and nitrogen, respectively. Reference materials were IAEA-N1 ($\delta^{15}N = 0.4 \pm 0.2$‰) and IAEA-CH-6 (sucrose) ($\delta^{13}C = -10.4 \pm 0.2$‰). Experimental precision (based on the standard deviation of one termite sample replicate used as internal standard) was 0.35 and 0.30‰ for carbon and nitrogen, respectively.

2.4. Data analysis

Pearson correlation was calculated at each site to test if $\delta^{13}C$ and $\delta^{15}N$ ratios were correlated. Between-site and between-species differences in $\delta^{13}C$ and $\delta^{15}N$ ratios were tested by a two-way ANOVA, with species and site as first and second factor, respectively. Both isotopes were analysed separately, using the four most frequently collected species at both sites. If sites differed in their isotopic values, between-site comparisons were performed for each species independently, using a Tukey post hoc test. Additionally, for species present in both sites, we tested if average $\delta^{13}C$ and $\delta^{15}N$ ratios for each species were correlated between sites. In order to test if *Anoplotermes*-group species differed in their feeding habits, we compared $\delta^{13}C$ and $\delta^{15}N$ values using a one-way ANOVA on both isotopes separately. The analyses were only undertaken on the Nouragues data, because insufficient data were available from Petit Saut. Each species with at least four occurrences was used in the analyses. If a significant difference was found, a Tukey post hoc test was performed to compare each pair of species separately. The feeding group concept of Donovan et al. (2001) was tested against $\delta^{15}N$ results using Student's t-test, both sites being treated separately. Results obtained on the wood feeder *H. tenuis* are shown for comparative purposes, but were never included in statistical analyses.

3. Results

Overall, 159 termite samples representing 26 species were collected: 62 samples representing 15 species were collected in Petit Saut, whereas 97 samples and 25 species were collected in Nouragues. The range of $\delta^{13}C$ values was -23.8 to -28.5‰ in Petit Saut (Fig. 1) and -25.1 to -29.1‰ in Nouragues (Fig. 2). $\delta^{15}N$ values ranged between 6.4 and 12.3‰ in Petit Saut (Fig. 1) and 7.5 and 16.5%,, in Nouragues (Fig. 2) for *Anoplotermes*-group species. By comparison, $\delta^{13}C$ and $\delta^{15}N$ ranges for the wood feeder *H. tenuis* were respectively -27.8 to -30.1‰ and 4.5-5.2‰ in Petit Saut ($n = 4$), -28.1 to -29.3‰ and 4.5-6.2‰ in Nouragues ($n = 9$). A positive correlation between $\delta^{13}C$ and $\delta^{15}N$ values was found at both sites (Nouragues: Pearson's $r = 0.295$, $p = 0.003$; Petit Saut: $r = 0.43$, $p = 0.001$).

The $\delta^{13}C$ and $\delta^{15}N$ values of 14 species, collected in both sites, were compared between Nouragues and Petit Saut. Of these, 4 species were collected frequently enough in both sites to allow statistical analysis at the species level. For none of them, termites collected in Petit Saut differed significantly in their $\delta^{13}C$ values from those collected in Nouragues (two-way ANOVA, second factor, sites: $F_{1,76} = 0.744$, $p = 0.479$). By contrast, termites collected in the two sites differed significantly in their $\delta^{15}N$ values (two-way ANOVA, second factor, sites: $F_{1,72} = 15.525$, $p < 0.001$). Taken individually, *Anoplotermes banksi* and *Anoplotermes* sp. *M* showed a significant difference in their $\delta^{15}N$ values, whereas the two other species, *Anoplotermes* sp. *C* and *Anoplotermes* sp. *U* did not (Tukey test: *A. banksi*: $q = 5.206$, $p < 0.001$; *A.* sp. *M*: $q = 7.259$, $p < 0.001$; *A.* sp. *C*: $q = 0.692$, $p = 0.626$; *A.* sp. *U*: $q = 1.014$, $p = 0.476$). When all species present in both sites were considered, the average $\delta^{13}C$ value of a species in Nouragues was not correlated to its $\delta^{13}C$ in Petit Saut (Pearson's $r = 0.160$, $p = 0.584$), where these values were more broadly dispersed (Bartlett test: $\chi^2 = 6.357$, df = 1, $p = 0.012$). By contrast, while all species collected from both sites showed a higher $\delta^{15}N$ value in Nouragues (Fig. 3), species-average $\delta^{15}N$ values for both sites were highly correlated ($r = 0.862$, $p < 0.001$), and did not show any difference in their dispersion (Bartlett test: $\chi^2 = 1.201$, df = 1, $p = 0.273$).

In total, 9 morphospecies were represented by 4 or more occurrences in Nouragues. Because we suspected that one of them, *Anoplotermes* sp. *E,* could actually encompass several closely similar species, we discarded this taxon from further analyses. *Anoplotermes*-group species differ significantly in their $\delta^{13}C$ and $\delta^{15}N$ values (one-way ANOVA: $\delta^{13}C$: $F_{7,48} = 2.819$, $p = 0.015$; $\delta^{15}N$: $F_{7,48} = 23.91$, $p < 0.001$). However, on the 28 pairwise comparisons carried out, not a single one was significant for $\delta^{13}C$ (Tukey test: $p > 0.05$) whereas 14 of them were significant for $\delta^{15}N$ (Tukey test: $p < 0.05$) (Fig. 2).

Some species are characterized by low values $\delta^{15}N$, barely higher than those of wood feeders. For instance, *Ruptitermes* nr. *silvestrii*, a species generally collected from pieces of wood, between bark and sapwood, displayed $\delta^{15}N$ values between 6.4 and 8.5. Two epigeous nest builders, the very abundant *A. banksi* and the less common *Anoplotermes parvus*, are also among the lowest $\delta^{15}N$ scores. There was no significant difference in $\delta^{15}N$ values between species assigned to feeding groups III and IV (Student t-test: Petit Saut: $t = 0.209$, df = 12, $p = 0.838$; Nouragues: $t = 1.063$, df = 22, $p = 0.299$).

Fig. 1. *Specific variation (mean ± SE) of $\delta^{13}C$ and $\delta^{15}N$ ratios in worker termites of the Anoplotermes-group collected in Petit Saut. SE is depicted for all species with 3 or more samples.*

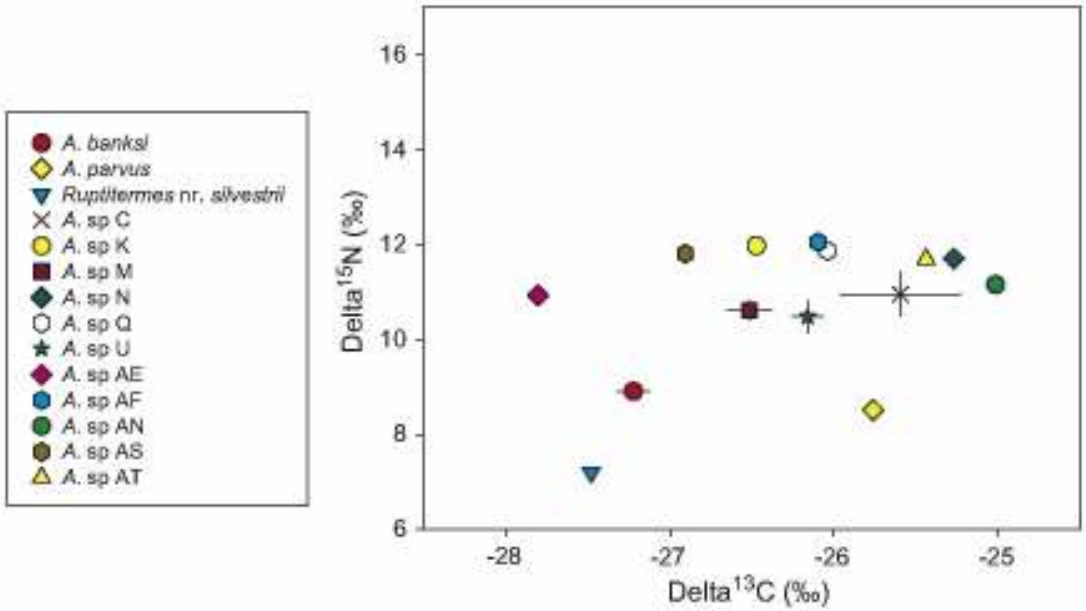


Fig. 2. *Specific variation (mean ± SE) of $\delta^{13}C$ and $\delta^{15}N$ ratios in worker termites of the Anoplotermes-group collected in the Nouragues Nature Reserve. SE is depicted for all species with 3 or more samples.*

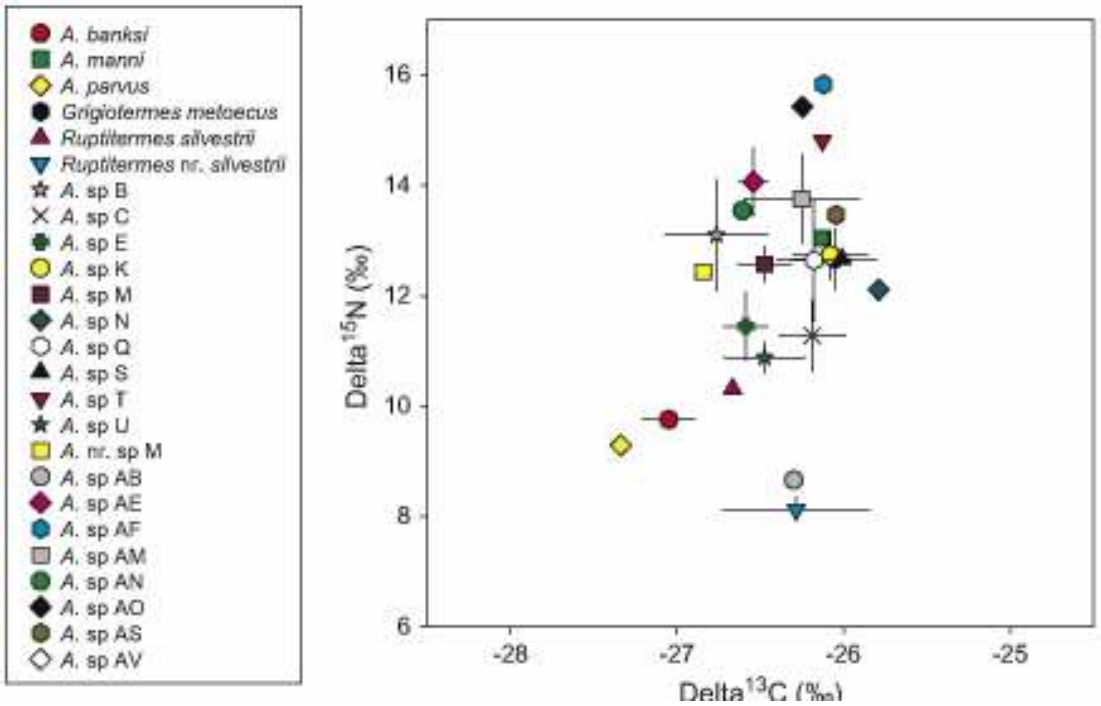
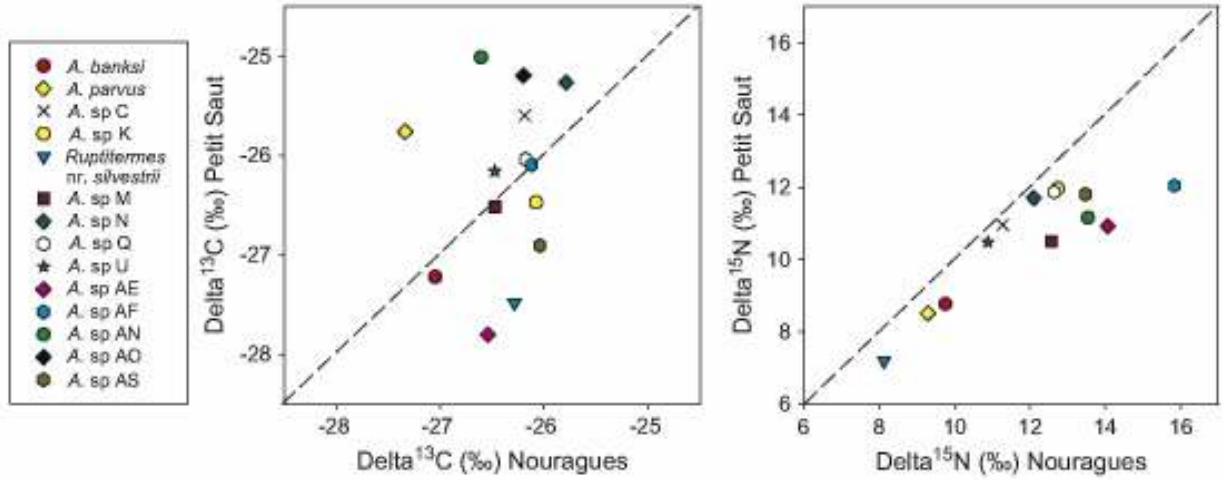


Fig. 3. *Species-average values of $\delta^{13}C$ and $\delta^{15}N$ ratios in worker termites, compared between Petit Saut and Nouragues. Dashed lines indicate equal $\delta^{13}C$ and $\delta^{15}N$ values for both sites.*



4. Discussion

All members of the subfamily Apicotermitinae are considered to be soil feeders, belonging to feeding groups III and IV of Donovan et al. (2001). This is well supported for the neotropical *Anoplotermes*-group species by generally high $\delta^{15}N$ signatures (mostly between 10 and 16.5), comparable to those found in soil feeders from tropical Africa (Tayasu et al., 1997), whereas $\delta^{15}N$ values for the wood feeder *H. tenuis* were, as predicted, lower ($\delta^{15}N$ = 4.5-6.2). However, some species of the *Anoplotermes*-group display relatively low $\delta^{15}N$ values, only slightly larger than those of *H. tenuis.* The fact that *R.* nr. *silvestrii* was collected from decayed wood, on which it presumably feeds, is consistent with the low $\delta^{15}N$ of this species. Among species with low $\delta^{15}N$ values are the two nest building species: *A. parvus* and *A. banksi.* The soil-feeding habits of *A. banksi* have however been confirmed by nest material analysis, which revealed higher proportions of heavy mineral particles than in nests

of presumed interface feeders such as *Termes* and *Embiratermes* species (Amelung et al., 2002).

Species collected from both sites differed in their average $\delta^{15}N$ values, which were slightly lower in Petit Saut than in Nouragues. This was also true for the wood feeder, *H. tenuis.* This suggests that sites slightly differ in the overall abundance of ^{15}N in the environment. Such spatial variability of soil $\delta^{15}N$ is commonplace, although it is rather low among French Guiana forests, as among tropical rainforests in general (Guehl et al., 1998; Martinelli et al., 1999). Interestingly, all species are not equally affected by intersite $\delta^{15}N$ variability. One explanatory hypothesis is a species-specific shift in food item selection according to the local pool of competitors. As different sites may host different termite communities, the precise quality of food a species is able to exploit may be influenced by competitors.

In both sites, we found highly significant differences in $\delta^{15}N$ values among species in the *Anoplotermes*-group. In addition, for species recorded from both Nouragues and Petit Saut, species-average $\delta^{15}N$ values from both sites were highly correlated. These interspecific variations and their reproducibility constitute strong evidence for feeding niche differentiation along a soil degradation gradient in the *Anoplotermes*-group, a phenomenon known to occur in other components of the soil fauna such as oribatid mites (Schneider et al., 2004) and collembolans (Chahartaghi et al., 2005; Hishi et al., 2007). Specialisation to a degradation state of soil organic matter therefore represents an important factor which can explain, at least partially, the coexistence of more than 30 humivorous termite species of this group in French Guiana forests (Davies et al., 2003b). We attempted to apply the anatomical criteria provided by Donovan et al. (2001) to distribute species between two feeding groups (III and IV), but this a priori classification was not supported by our isotopic analysis: species appear distributed along a continuum of $\delta^{15}N$ values rather than in two clusters, and no significant difference was found between species a priori classified in group III versus group IV. The value of this distinction deserves to be re-examined over a broader range of soil-feeding taxa.

The *Anoplotermes*-group (Apicotermitinae), though rich in species, co-exists with a broad array of other presumed soil-feeding termites from other subfamilies, such as the *Termes*-group (Termitinae), *Neocapritermes* spp. (Termitinae), the *Armitermes*-group (mandibulate nasutes, Syntermitinae) and the *Subulitermes*-group (full nasutes, Nasutitermitinae). For instance, on 100 termite species recorded from St Eugène, French Guiana, Davies et al. (2003b) found 34 species of the *Anoplotermes*-group and 39 other soil feeders. Whether different clades of humus feeders occupy clade-specific niches, or whether every clade has diversified to encompass a range of food sources, as suggested for the *Anoplotermes*-group, deserves further investigation. In any case, it is likely that the higher diversity of soil-feeding termites compared to wood-feeding ones observed in neotropical and African rainforests (Eggleton et al., 1996, 2002; Davies et al., 2003a), even when the wood feeders of the canopy are considered (Roisin et al., 2006), is related to narrower niche specialisation belowground. Our results support the hypothesis that niche availability increases along the humification gradient from sound, recently fallen litter to fully humified soil organic matter (Brauman et al., 2000).

Our results indicated that $\delta^{13}C$ and $\delta^{15}N$ values are correlated in both sites. This was expected as both isotopic values are generally known to increase down the soil profile. However, the two isotopes are not equally discriminant, as $\delta^{13}C$ values did not provide reproducible interspecific differences. This suggests that soil-feeding *Anoplotermes*-group termites are not very selective regarding the origin of the organic matter they feed on. Alternatively, any specific preferences may be blurred by non-linear change in $\delta^{13}C$ during organic matter degradation, a broadly documented process (review in Tiunov, 2007). This may restrict the usefulness of $\delta^{13}C$ analysis to the differentiation between consumers of organic matter derived from plant material of grossly different ^{13}C content, such as C3 versus C4 plants.

Acknowledgments

We are grateful to Philippe Cerdan and the staff of the Laboratoire Environnement de Petit Saut for logistical help. We would also like to thank Patrick Chatelet and Wemo Betian of the Nouragues scientific station for providing facilities. Financial support was provided by the Fund for Scientific Research (F.R.S.-FNRS), Belgium, through travel grants and a predoctoral fellowship to T. Bourguignon; by project of the Czech Academy of Sciences to J. Šobotník; by the Université Antilles-Guyane through a predoctoral fellowship to J.-M. Martin; and by the French CNRS, through project Amazonie II (Prof. Alain Dejean).

Published in: Soil Biology & Biochemistry (2009), vol. 41, pp. 2038-2043.
Status: Postprint (Author's version)

Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.soilbio.2009.07.005.

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